

## ADAPTIVE PHYSIOLOGY OF HETEROMYID RODENTS<sup>1</sup>

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**ABSTRACT.**— Heteromyid rodents are distributed from the New World tropics to the deserts of North America, but their habitation of deserts is relatively recent. Their evolutionary history, though, is associated with progressive aridity, with larger quadrupedal taxa being more mesic (and primitive), and smaller quadrupeds and all bipeds more xeric. The correlation between water regulatory efficiency and body mass is strongly negative in heteromyids; bipedal *Dipodomys* spp. have water regulatory efficiency fixed at an intermediate level independent of mass. Heteromyids generally have basal metabolic rates reduced below the eutherian level, with the greatest reductions occurring in desert species. The use of torpor as an energy-conserving device is cosmopolitan in small (< 40 g) heteromyids, but is inconsequential or lacking in larger ones. Bipedalism, characteristic of *Dipodomys*, confers no direct energetic advantages as revealed in treadmill studies.

Large quadrupedal heteromyids have adaptive physiologies suitable for more mesic habitats, but smaller quadrupeds are suited for xeric existences; these characteristics likely reflect an evolution from a tropical ancestry to rather recent habitation of deserts. Bipedalism occurs only in xeric-adapted forms and has no directly discernible energetic benefit; yet it appears to relieve in some unknown way the energetic constraints of foraging.

The genera and species of the family Heteromyidae are distributed along a pronounced gradient of water availability in the New World ranging from the wet tropics of Central and South America to the driest deserts of North America (Hall 1981). This present-day distribution mimics the paleoclimatological history of the family, starting with a tropical ancestry, followed by an adaptive radiation throughout the Tertiary in response to progressive aridity and seasonality of rainfall, and culminating in the diverse fauna of desert heteromyids with which we are so familiar (Axelrod 1958, Hall 1981, Reeder 1956, Wood 1935). With this in mind, it is my contention that tropical heteromyids may be viewed at least ecologically as ancestral models of early heteromyids, the desert forms as advanced derivatives, and those occupying intermediate habitats as transitional forms. Thus, extant species should provide us with important clues concerning the evolutionary and ecological trajectories of the family at the levels of physiology, morphology, and behavior.

The quadrupedal heteromyid genera (*Heteromys*, *Liomys*, *Perognathus*), at least with respect to locomotion, are the more general-

ized, and the bipedal members (*Dipodomys*, *Microdipodops*) are the more specialized. In addition, the quadrupedal members span the entire distributional range and nearly the entire size range of the family, but the bipedal forms are confined to semiarid and arid habitats, and (with the exception of the small-in-size *Microdipodops*) occupy the upper portion of the size spectrum (Hall 1981). By inspection (Hall 1981), there is a strong positive correlation within the quadrupedal heteromyids between body size and moistness of the habitat, suggesting that reductions in body mass may confer a selective advantage upon quadrupedal heteromyids living in more arid habitats; on the other hand, the arid-adapted bipeds are commonly relatively large and show no apparent relationship between the body mass of individual species and habitat aridity, suggesting a linkage between bipedality and aridity independent of body mass.

Herein, I explore certain aspects of water and energy regulatory physiology of heteromyid rodents, paying particular attention to patterns related to habitat, body mass, and/or locomotor mode.

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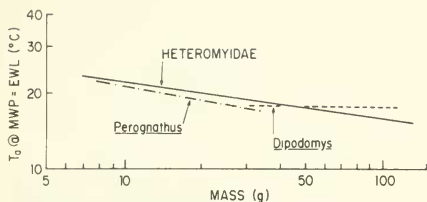


Fig. 1. The double logarithmic relationships between water regulatory efficiency ( $T_a$  @ MWP = EWL) and body mass in 5 genera and 13 species of heteromyid rodents. Regression lines are provided for all species (solid line) and *Perognathus* spp. (dot-dash line), and both have significant slopes ( $F$  test,  $P < .05$ ). The horizontal line (dashed) represents the average value for all *Dipodomys*, which did not have a significant regression. The regression lines are fit to all the values for each species; the regression equations are  $T_a$  @ (MWP = EWL) =  $29.682g^{-0.137}$  in all 13 heteromyid species, and  $T_a$  @ (MWP = EWL) =  $31.078g^{-0.166}$  in *Perognathus* spp.; the mean value for *Dipodomys* spp. is  $18.1 \pm SD 0.6$  C. The heteromyid species employed span the geographic, climatological, and body mass ranges of the family and include *Dipodomys deserti*, *D. merriami*, *D. ordii*, *D. panamintinus*, *Heteromys desmarestianus*, *Liomys irroratus*, *L. salvini*, *Microdipodops megacephalus*, *Perognathus baileyi*, *P. fallax*, *P. flavus*, *P. hispidus*, and *P. longimembris*. After MacMillen and Hinds (in press).

### WATER REGULATORY EFFICIENCY

Numerous accounts in the literature attest to the relatively great powers of water conservation in heteromyid rodents, and indicate that the arid-adapted forms (*Dipodomys*, *Microdipodops*, *Perognathus*) are conservative often to the point of exogenous water independence (MacMillen 1972, Schmidt-Nielsen et al. 1948; pers. obs.), and the more mesic adapted forms (*Heteromys*, *Liomys*) are less conservative in their water economies and require dietary augmentation of exogenous water (Hudson and Rummel 1966, Fleming 1977). I (MacMillen 1983) have argued that the conservative nature of heteromyid water economy, regardless of habitat, is likely linked to the family's dietary specialism, granivory: this is because rodents in particular depend upon a common resource packet to meet nutrient, energy, and water needs, and those that use the driest packets (seeds) are the most conservative in their water economies.

With the supposition that heteromyids are relatively conservative in their water economies, and that, at least for the quadrupedal

species, body mass might be positively correlated with moistness of the habitat and negatively correlated with economical water regulation, MacMillen and Hinds (1983) undertook an examination of water regulatory efficiency in extant heteromyids that included both quadrupedal and bipedal members across the entire taxonomic, distributional, and size ranges of the family. This examination was based on a model that predicted that water regulatory efficiency is negatively related to body mass and positively related to ambient temperature. Our criterion of water regulatory efficiency is that ambient temperature ( $T_a$ ) at which the major avenue of water input (metabolic water production, MWP) just balances the major avenue of water output (evaporative water loss, EWL). Thus, the model predicts that those species achieving water balance (MWP = EWL) at the highest  $T_a$ s are the most efficient in water regulation, being able to subsist exclusively on air-dry seeds to meet both energy and water needs while active on the surface even under warm conditions. A test of the model in which we evaluated simultaneously MWP and EWL from  $T_a = 5$ –35 C in 117 individuals, 13 species and 5 genera of heteromyids, confirms our predictions for the family in general (Fig. 1). However, when the two most speciose genera (*Perognathus*, *Dipodomys*) are treated separately, *Perognathus* spp. conform even more strongly (possess a steeper slope) to the model, but in *Dipodomys* spp. water regulatory efficiency is fixed at an intermediate level independent of body mass (Fig. 1). This intergeneric break in patterns of water regulatory efficiency coincides with a break in body mass (ca 35g) and a break in locomotor mode, points whose relevances will be discussed later in this paper.

### BASAL METABOLIC RATE

It has long been known that the basal metabolic rates (BMR) of mammals are logarithmically correlated with body mass (Kleiber 1932). This scaling of BMR with body mass in mammals was statistically refined by Brody (1945) and Kleiber (1961) to provide indistinguishable regression equations for predicting BMR for mammals of any known mass:  $BMR (cm^3 O_2/g \cdot h) = 3.8 W(g)^{-0.27}$

(Brody 1945) or  $M = 3.5W^{-0.25}$  (Kleiber 1961; see MacMillen and Nelson 1969 for conversion of equations from animal-specific to mass-specific values). Rodents, too, conform in general to these allometric expectations (Morrison 1948), but Dawson (1955) was the first to suggest that heteromyid rodents may have BMR reduced below the expected levels. Hudson and Rummel (1966) confirmed this suggestion for the subtropical species *Liomys salvani* (= *L. salvini*?) and *L. irroratus*; more recently McNab (1979) has shown through a search of the literature and his own measurements that, of the heteromyid species for which measurements were available (12 species, all 5 genera), only a tropical *Heteromys* (*H. anomalus*) possessed a BMR at or exceeding the Kleiber prediction—all others were reduced. Furthermore, McNab's (1979) analysis revealed the BMRs of *Perognathus* spp. were not only reduced, but also were independent of body mass; it is interesting to note that the four *Perognathus* measurements were from four different laboratories.

Our studies of water-regulatory efficiency as described above and in MacMillen and Hinds (1983) provide a rich data base from a single laboratory for comparing mass-related aspects of water and energy metabolism both within the family Heteromyidae, and with eutherian mammals in general. We are preparing a major synthesis of heteromyid metabolic allometry (Hinds and MacMillen, in preparation), and so the following summarize only briefly the most pertinent information related to BMR.

Because our criterion of water regulatory efficiency required that our animals be oxidizing food of known composition at the time of measurement of oxygen consumption ( $\dot{V}_{O_2}$ ), our animals were not postabsorptive when measured in thermal neutrality, and hence did not conform strictly to the requirements for BMR. The animals were oxidizing millet (81.4 percent carbohydrate, 5.1 percent lipid, 13.5 percent protein), which should elevate metabolic rate due to the specific dynamic action (SDA) of food utilization by about 9 percent above basal levels (Brody 1945). In spite of the possible influence of SDA on metabolic rate of our specimens, it is apparent that the basal metabolic rate of the

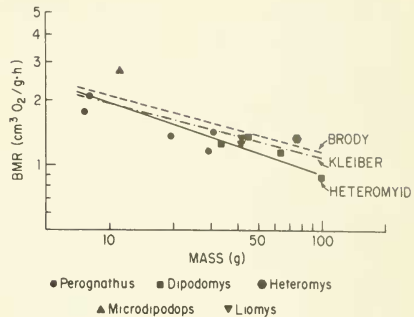


Fig. 2. The double logarithmic relationship between mass-specific basal metabolic rate and body mass in heteromyid rodents, using the same species as indicated in Figure 1. The dashed line is the allometric expectation for eutherian mammals from Brody (1945); the dot-dash line is the expectation for eutherians from Kleiber (1961). The solid line is fit to the data for heteromyids by the regression equation  $BMR = 3.69 W(g)^{-0.28}$  ( $S_{yx} = .010$ ,  $S_b = .028$ ,  $r^2 = 0.504$ ). The geometric symbols represent different genera as indicated on the figure. The BMR values employed in this analysis are the two lowest measures of  $\dot{V}_{O_2}$  for each individual at that  $T_b$  in thermal neutrality for which the mean  $\dot{V}_{O_2}$  of that species was lowest (after Hinds and MacMillen, in preparation; data collection as in MacMillen and Hinds, in press).

heteromyids we tested is depressed below the values predicted by either the Brody (1945) or Kleiber (1961) relationships (Fig. 2).

Correcting for SDA would yield even greater depressions. The slope of the regression line relating BMR to mass of heteromyids (-0.28) is statistically indistinguishable from that of Brody (-0.27) and Kleiber (-0.25). Using the raw data of Brody (1945), a direct comparison can be made of elevation between his and the heteromyid data sets, which shows that, at the mean body mass (ca 30g) of the heteromyids employed, heteromyid BMR is significantly ( $P < .05$ ) reduced by 11 percent of that predicted for eutherian mammals in general (following method of comparing elevations by Snedecor 1956 and Zar 1974). Of the 13 heteromyid species included in Figure 2, 5 (*Dipodomys deserti*, *D. merriami*, *Perognathus baileyi*, *P. fallax*, *P. longimembris*) are from severe desert scrub habitats, and their BMR collectively is reduced by 24 percent below that predicted for eutherians.

Lastly, the 5 *Perognathus* spp. conform strongly to the relationship between BMR and body mass, with no indication of the mass-independent relationship reported by McNab (1979) on data emanating from several laboratories. Since two of the four *Perognathus* species included in McNab's (1979) analysis were also employed in ours (*P. longimembris*, *P. hispidus*) the discrepancy is likely due to interlaboratory differences in measuring BMR rather than to interspecific deviations in metabolism. This attests to the importance of using only data collected from a single laboratory when undertaking metabolic comparisons at lower taxonomic levels.

Thus, it is concluded that heteromyid rodents have reduced BMR (and metabolic rates in general) and that the reductions are not only recognizable at the taxonomic level, but are most pronounced in those members living under more arid conditions.

#### BIPEDAL LOCOMOTION

The fact that heteromyids are divided in locomotor habits into quadrupedal and bipedal forms, and that the latter are confined to semiarid and arid habitats within the family distribution, suggests the presence of advantages inherent in bipedalism that favor an arid existence. Howell (1933) observed that *Dipodomys* occurred predominantly in open terrain, where bipedality conferred a combination of fast, erratic movements and balance that enhanced predator escape to the extent "that no mammal can catch this rodent in fair chase, but only in stealth." Also favoring the hypothesis that bipedality in *Dipodomys* aids primarily in predator escape and avoidance were Bartholomew and Caswell (1951), who stated "the entire economy of the animal is set up for efficient evasion of danger in areas relatively devoid of cover, which emphasizes that survival in this species has been dependent upon a series of mutually supporting adaptations of which its locomotor equipment is the most obvious."

Recently, investigators have measured the actual costs of locomotion through indirect calorimetry of mammals running on treadmills. These studies have concentrated on quadrupedal running and show considerable uniformity in the scaling of energetic costs to

body mass (Taylor et al. 1970). The first suggestion that bipedal hopping might confer unusual energetic benefits was by Dawson and Taylor (1973), who reported that red kangaroos, while hopping, effectively had energetic costs that were independent of running speed, i.e., a bipedal plateau. Shortly thereafter Fedak et al. (1974) reported data suggesting that for small animals (< 1000g) the cost of transport for bipeds (exclusively birds) is less than that for quadrupeds (exclusively mammals). This contention was reversed by Fedak and Seeherman (1979) and Paladino and King (1979), who demonstrated independently, using a more extensive data set including quadrupedal mammals and lizards and bipedal birds and mammals, that there is no difference in the scaling of energy requirements for locomotion between bipeds and quadrupeds, but only differences between clumsy and graceful runners. But these latter studies, as opposed to Dawson and Taylor's (1973) with the kangaroo, employed animals that were either two-legged bipeds (primates and birds) or four-legged quadrupeds (other mammals and lizards), and not mammals that at slower running speeds are pentapedal (kangaroos) or quadrupedal (for example, heteromyids), but then become bipedal at faster speeds.

Dawson (1976) and Baudinette et al. (1976) measured the energetic costs of locomotion in two species of Australian murid hopping mice (*Notomys cervinus* and *N. alexis*, respectively) that are ecological and physiological equivalents to bipedal heteromyids (MacMillen and Lee 1969, 1970). Both species had similar patterns relating oxygen consumption ( $V_{O_2}$ ) to running speed with a positive linear relationship at slower speeds (< 2.0 km/h) and a plateau at higher speeds (> 2.0 km/h). Dawson (1976) reports intermittent use of both quadrupedal running and bipedal hopping at plateau speeds, but Baudinette et al. (1976) report only quadrupedal running. In addition, Dawson (1976) suggests that the plateau in *N. cervinus* is aerobic and therefore represents a real energetic savings related to elastic energy storage compared to that during strictly quadrupedal running. Baudinette et al. (1976) are less committal and imply that the plateau may be either an aerobic one dependent upon elastic storage,

or it may be purely anaerobic, occurring at the level of maximal aerobic capacity. Clearly this plateau can represent an energy-conserving mechanism only if aerobic.

My recent treadmill studies of the metabolic cost of locomotion in small bipedal and quadrupedal mammals have concentrated on heteromyid rodents. Initial results that compare running and hopping costs of four species of small bipeds (0.03 to 3.0 kg; Rodents: Heteromyidae: *Dipodomys merriami*, *D. deserti*; Pedetidae: *Pedetes capensis*; Marsupialia: Macropodidae: *Bettongia penicillata*) show no aerobic bipedal plateau while hopping at any of the speeds tested. Further, a plateau could be induced in poorly trained individuals that ran in an oscillatory manner, but this disappeared when they were trained to run smoothly (Thompson et al. 1980).

To confirm further the presence or absence of a bipedal plateau in *Dipodomys* spp., simultaneous measurements of  $\dot{V}_{O_2}$  and  $\dot{V}_{CO_2}$  were made in *D. ordii* while running on a treadmill, and of blood lactate immediately after running. The results are reported in Figure 3. At low running speeds (<3.0 km/h)  $\dot{V}_{O_2}$ ,  $\dot{V}_{CO_2}$ , and blood lactate are positively and linearly related to speed. At higher running speeds (> 3.0 km/h)  $\dot{V}_{O_2}$  plateaus distinctly,  $\dot{V}_{CO_2}$  continues to increase linearly but with a shallower slope, and blood lactate continues to increase sharply, but with the possibility of a plateau at 4.0 and 5.0 km/h.

At running speeds above 4.0 km/h there is a distinct decline in the willingness of individuals to run, with typically less than one-half of the individuals that readily ran at lower speeds willing to run at the higher speeds sufficiently long (2-3 min) to reach steady state. It is unlikely that this unwillingness to run at higher speeds for even short periods of time was due to hyperthermia. As Wunder (1974) has noted, no inhibition of running in *D. ordii* accompanied moderate hyperthermia while running at lower speeds ( $\leq 1.8$  km/h), but did for prolonged periods of time (10-15 min). The transition from quadrupedal to bipedal running occurs between 3.0 and 4.0 km/h, with most of the  $\dot{V}_{O_2}$  plateau coincident with bipedal locomotion.

I am convinced, however, that the  $\dot{V}_{O_2}$  plateau depicted in Figure 3 is anaerobic, and therefore cannot be construed as an

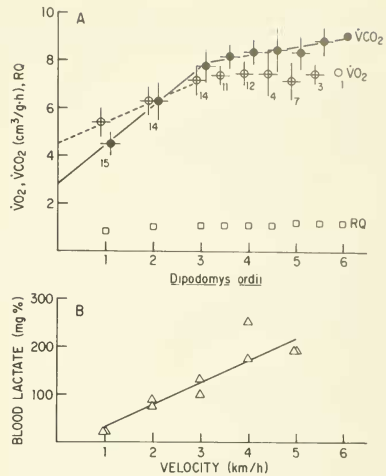


Fig. 3.A. The relation between oxygen consumption ( $\dot{V}_{O_2}$ ) and carbon dioxide production ( $\dot{V}_{CO_2}$ ) and velocity in *Dipodomys ordii* running on a treadmill at  $T_a = 20^\circ C$ . The treadmill was enclosed in a Plexiglas chamber through which air was pulled at a rate of 4.1 L/min.  $\dot{V}_{O_2}$  and  $\dot{V}_{CO_2}$  were measured with an Applied Electrochemistry S-3A oxygen analyzer and an Infrared Industries carbon dioxide analyzer. All measurements were corrected to STPD. The dashed line is fit to the  $\dot{V}_{O_2}$  data between 1 and 3 km/h by linear regression analysis and is described by the equation  $\text{cm}^3/\text{g}\cdot\text{h} = 0.91(\text{km}/\text{h}) + 4.46$  ( $S_x = 0.55$ ,  $S_y = 0.60$ ,  $r^2 = 0.64$ ); the line has a significant positive slope ( $F$  test,  $P < .05$ ). The solid line is fit to the  $\dot{V}_{CO_2}$  data between 1 and 3 km/h, and between 3 and 6 km/h. Both have significant slopes, and are described by the equations  $\text{cm}^3/\text{g}\cdot\text{h} = 1.65(\text{km}/\text{h}) + 2.88$  ( $S_x = 0.67$ ,  $S_y = 0.43$ ,  $r^2 = 0.81$ ) and  $\text{cm}^3/\text{g}\cdot\text{h} = 0.36(\text{km}/\text{h}) + 6.83$  ( $S_x = 0.58$ ,  $S_y = 0.89$ ,  $r^2 = 0.21$ ). The numbers represent the number of measurements obtained at each speed from a total of 13 individuals. Solid circles represent mean  $\dot{V}_{CO_2}$  measurements, hollow circles represent mean  $\dot{V}_{O_2}$  measurements, vertical lines represent the interval  $\bar{X} \pm 1$  SD, and hollow squares represent mean RQ values ( $\dot{V}_{CO_2}/\dot{V}_{O_2}$ ).

B. The relation between blood lactate and velocity in *D. ordii* running on a treadmill at  $T_a = 20^\circ C$ . Each animal was allowed to run at one speed for 2-5 min during measures of  $\dot{V}_{O_2}$  and  $\dot{V}_{CO_2}$ , and these measurements are included in the data depicted in Fig. 3A. It was then immediately removed, a blood sample was taken from the orbital sinus within 30 sec of removal, and the whole blood placed in perchlorate solution. Lactate concentration was determined using a Boehringer-Mannheim lactate test kit. Each hollow triangle represents one value from a different individual, with a total of ten values (individuals). The solid line is fit to the data by regression analysis and is described by the equation  $\text{mg}\% = 46.234(\text{km}/\text{h}) - 13.635$  ( $r^2 = 0.825$ ); the slope is significant ( $F$  test,  $P < .05$ ).

energy-conserving mechanism. The mean  $\dot{V}_{O_2}$  between 3.0 and 6.0 km/h ( $7.34 \pm \text{SD } 0.57$   $\text{cm}^3/\text{g}\cdot\text{h}$ ;  $N=52$ ) falls within the 95 percent confidence intervals predicted for maximal aerobic capacity ( $\dot{V}_{O_2}$  max) in a small mammal ( $\bar{X}$  body mass = 52.7 g) from Lechner's (1978) allometric relationship:

$$\dot{V}_{O_2} \text{ max} = 0.499 W^{.675}$$

( $\dot{V}_{O_2}$  is in  $\text{cm}^3/\text{min}$ , and  $W$  is mass in g).

The mean  $\dot{V}_{O_2}$  for *D. ordii* between 3.0 and 6.0 km/h, however, falls below the 95 percent confidence intervals for  $\dot{V}_{O_2}$  max as predicted by Taylor et al. (1980):

$$\dot{V}_{O_2} \text{ max} = 1.92 W^{.809}$$

( $\dot{V}_{O_2}$  is in  $\text{cm}^3/\text{sec}$ , and  $W$  is mass in kg).

Lechner's (1978) relationship included  $\dot{V}_{O_2}$  max induced by cold, helium-oxygen mixtures or running, in 14 small mammals species (< 2.6 kg), 11 of which were rodents. Taylor et al. (1980) confined their measurements to treadmill running, with the majority of their mammals large (> 2.6 kg) or very large; of the 21 species for which measurements are reported, only 4 are rodents while 11 are ungulates. It is difficult to resolve the discrepancies between these two relationships, as their data bases differ taxonomically, methodologically, and by body mass. Our protocol is most similar to that of Lechner (1978) in terms of taxonomy and body mass, and resembles that of Taylor et al. (1980) methodologically.

Additional confirmation that the  $\dot{V}_{O_2}$  plateau reported above for *D. ordii* is anaerobic comes from the analysis of blood lactate following running at the highest speeds tested. The mean of four values for *D. ordii* after running 2-3 min at 4.0 and 5.0 km/h is  $201.9 \pm \text{SD } 34.8$  mg percent. This mean, and three of the four values fall within the 95 percent confidence intervals around the mean ( $190.7 \pm \text{SD } 9.1$  mg percent) of blood lactate levels of 9 mammalian species running on treadmills at  $\dot{V}_{O_2}$  max, as reported by Seeherman et al. 1981. The fourth value lies above the confidence intervals. Thus, it is apparent from the perspectives of  $\dot{V}_{O_2}$  and blood lactate levels that the bipedal plateau we observed in *D. ordii* is anaerobic. Finally, Biewener et al. (1981) have examined with

the use of force plates and X-ray cinematography bipedal hopping in *Dipodomys spectabilis* and conclude that elastic storage of energy in this kangaroo rat is much less than in kangaroos.

The adaptive significance of bipedality in heteromyids has yet to be demonstrated with rigorous laboratory and field tests. The most plausible current explanation is the original one proposed by Howell (1933) and Bartholomew and Caswell (1951) that bipedality aids in predator avoidance and escape. I believe it is additionally possible that bipedality confers other locomotor advantages not readily translatable into energetic currency, such as enhancing acceleration and burst speeds. These ideas have yet to be tested.

#### USE OF TORPOR

Torpor (or natural hypothermia), in which body temperature and energy metabolism are reduced well below normothermic levels, either on a circadian basis or for longer periods, is well documented in virtually all heteromyids whose mean body masses are typically less than 40 g (i.e., all *Perognathus* spp., *Microdipodops pallidus*, and *M. megacephalus*, pers. obs., Bartholomew and Cade 1957, Bartholomew and MacMillen 1961, Cade 1964, Tucker 1965, Wang and Hudson 1970, Wolff and Bateman 1978). In larger quadrupedal heteromyids (i.e., *Heteromys*, *Liomys*) torpor has not been observed (pers. obs., Fleming 1977, Hudson and Rummel 1966). Torpor appears to be a weakly developed capacity in *Dipodomys*, having been documented in *D. merriami* (Dawson 1955, Carpenter 1966, Yousef and Dill 1971), *D. panamintinus* (Dawson 1955) and observed in *D. deserti* (pers. obs.). In all instances torpor in *Dipodomys* spp. was induced by starvation and/or cold stress, and frequently resulted in death during torpor or after arousal. In the few *Dipodomys* spp. in which torpor has been documented it appears to be best (but still weakly) developed, as a circadian phenomenon, in the smallest species, *D. merriami* ( $\geq 35$  g). I have seen no convincing evidence that torpor in *Dipodomys* spp. is an ecologically meaningful phenomenon.

Among *Perognathus* spp., there appear to be two prevailing patterns in the use of torpor: (1) those that employ it as an emergency

energy-conserving mechanism for short periods of time (one to several days) to avoid temporarily inhospitable surface conditions (*P. californicus*, Tucker 1962; *P. flavus*, Wolff and Batemann 1978); and (2) those that are or nearly are obligate hibernators, and abandon surface activity for several months each winter (*P. longimembris*, Kenagy 1973; *P. parvus*, Meehan 1976). The determinants of one pattern or the other are unknown, but they are not taxonomic because both patterns occur in each subgenus. In *Microdipodops* spp., torpor appears to be employed on a short-term basis, as both species can be trapped all year, even during winter on sub-freezing nights, except for those occasions when the substrate is frozen (Brown and Bartholomew 1969, Hall 1946; pers. obs.). In both *Perognathus* and *Microdipodops*, as in *Dipodomys*, the periodicity of torpor seems to be based on a circadian schedule with individuals initially torpid during the usual daylight hours and normothermic at night (Brown and Bartholomew 1969, Carpenter 1966, French 1977, Meehan 1976, Tucker 1962). If conditions that foster the use of torpor prevail, whether it be in obligate hibernators or short-termers, circadian bouts of torpor may extend into those of greater duration, some lasting several days (Brown and Bartholomew 1969, French 1977, Meehan 1976). Whether torpor be circadian or of longer duration, or whether the use of torpor bouts be confined to short periods of inhospitable surface conditions or to a complete winter season, its adaptive significance to these granivores is linked primarily to energy conservation, enabling its practitioners to subsist for short or longer periods in underground burrows on a finite energy store in the form of seed hoards at a fraction of the energetic cost they would expend if continually normothermic (Brown and Bartholomew 1969, Kenagy 1973, Meehan 1976, Tucker 1966).

For torpor to serve efficiently as an energy-conserving mechanism in heteromyids, its use must be accompanied by precision of control. Such precision has been demonstrated in *Microdipodops pallidus* by Brown and Bartholomew (1969), who have shown that periodicity and duration of torpor

bouts is related to ambient temperature and food supply in such a way that individuals invariably maintain body weight and accumulate seeds, even at very low temperatures and on seed rations reduced considerably below the normothermic requirement. An additional example of precision of energetic control while using torpor is seen in *Perognathus parvus* (Meehan 1976). This species is an obligate hibernator, and in Great Basin habitats in California is dormant in burrows typically from November through March, employing periodic bouts of torpor that may last as long as eight days interrupted by only brief (< one day) periods of arousal. In the laboratory during winter months *P. parvus* establishes large seed hoards (i.e., an energy surplus) and, while maintained at ambient temperatures equivalent to winter burrow temperatures (ca 5 C), spontaneously enters torpor; torpor bouts are initially circadian followed by progressive increases in duration until, commonly, individuals are torpid for five or more days at a time. Meehan's data under simulated winter conditions indicate that individuals are torpid, with body temperature ( $T_b$ ) approximating  $T_a$ , 90 percent of the time, and expend only 16 percent of the energy that would be expended if normothermic in an insulated nest in the burrow; this energy savings would obviously be increased several-fold if compared with the cost of nightly foraging on the surface.

The magnitude of energetic savings while torpid is demonstrated in Figure 4, which shows that at  $T_a = 2$  C (approximating winter burrow temperatures) the metabolic cost for torpid mice is 3 percent of that for resting nontorpid animals. The extraordinary precision of thermoregulatory control while torpid is also demonstrated in Figure 4: at  $T_a$ s between 2 and -2 C (and at a  $T_b$  barely above freezing) *P. parvus* is capable of activating the heat production machinery sufficient to maintain  $T_b$  at or slightly above 2 C. Thus, with tissues approaching freezing, these animals are capable of maintaining a constant body temperature at very low metabolic cost, thereby avoiding prohibitively costly normothermia and at the same time ensuring continuing survival throughout a winter season of underground dormancy.

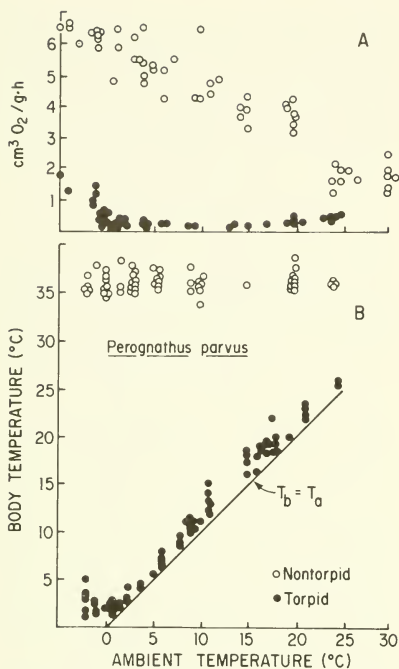


Fig. 4.A. The relation between oxygen consumption and ambient temperature in normothermic (hollow circles) and torpid (solid circles) *Perognathus parvus*. Normothermic values based on 59 measurements from 14 individuals; torpid values on 48 measurements from 12 individuals. After Meehan (1976).

B. The relation between body temperature ( $T_b$ ) and ambient temperature ( $T_a$ ) in normothermic (hollow circles) and torpid (solid circles) *P. parvus*. Normothermic values on 62 measurements from 19 individuals; torpid values on 78 values from 25 individuals. The solid line indicates where  $T_b = T_a$ . After Meehan (1976).

#### DISCUSSION AND CONCLUSIONS

As stated in the introduction, it is believed that close attention to extant heteromyids distributed over the geographic (i.e., climatic), size, and locomotor ranges of the family should reveal not only specifics about the daily lives of present-day populations and species, but also about the development of biological patterns over evolutionary time. With this in mind, the patterns of heteromyid physiology described above will be explored and an attempt will be made to place them in an evolutionary perspective with the following scenario.

Heteromyids arose in the early Tertiary New-World tropics (Reeder 1956, Wood 1935) as rather large ( $\geq 70$  g) quadrupedal granivores/frugivores whose cheek pouches enhanced foraging success for a single resource packet (seeds and/or fruits) that provided virtually all nutritional needs. These ancestral heteromyids would have possessed powers of water regulation consistent with the amount of preformed + oxidative water yielded from the food, and equivalent to that predicted for a quadrupedal heteromyid of that mass as depicted in Figure 1. At the time of their origin they likely possessed a BMR close to that typical of eutherian mammals, as in *Heteromys* and *Liomys* (Fig. 2).

From the heteromyid origin throughout the remaining Tertiary, the geographic region of heteromyid evolution (southwestern North America) was subjected to progressive aridity and seasonality of rainfall (Axelrod 1958); this was most pronounced in areas occupied by today's deserts (i.e., around  $30^{\circ}$  N latitude) and less pronounced with proximity to the equator. The progression of aridity and seasonality of rainfall would have resulted in shorter growing seasons, reduced primary production, and vegetational emphasis on seasonal seed production (rather than fruit) as a reproductive strategy. I envision the heteromyid responses to these climatic and biotic changes to include tracking the increases in aridity and accompanying temporal and volumetric reductions in seed production with reductions in body mass; such reductions in mass would promote increases in water-regulatory efficiency consistent with water yield (MWP) from a dry foodstuff (as seen in Fig. 1) and decreases in absolute energy needs per individual. Concomitant with this would have been reductions in BMR (and overall energy metabolism) comparable to those observed in Figure 2, thereby even further decreasing absolute energy needs in habitats with more limited seed production. The trade-off for decreases in body mass in these still quadrupedal forms would have been an increase in mass-related locomotor costs (Taylor et al. 1970), offset at this stage by reductions in BMR and continuing enhancement in foraging efficiency promoted by the use of cheek pouches. According to my scenario, species that are physiologically (and



ecologically) ancestral and transitional would have persisted through the present in habitats of appropriate rainfall and seed production patterns, most typically in tropical and subtropical settings.

The next sequence of events followed continuing reductions in mass of quadrupedal heteromyids down to about 35–40 g, at which some critical event(s) occurred, resulting in the locomotor dichotomy between quadrupedality and bipedality (and the eventual origins and adaptive radiations of *Perognathus* and *Dipodomys*). During the development of this dichotomy, water regulatory efficiency became fixed at an intermediate level and independent of mass in *Dipodomys*; in *Perognathus*, as in other quadrupedal heteromyids, water regulatory efficiency continued to increase concomitant with further reductions in body mass as the prevailing pattern of increasing aridity continued. Also, it is suspected that the capacity for torpor was developed just prior to the dichotomy in locomotion, and at some critical, relatively small mass (ca 40 g) at which the costs of quadrupedal foraging during periods of excessive energy demand (low temperatures and/or reduced seed availability) exceeded the benefits. Torpor would represent a physiological alternative to relieve either temporarily or for longer periods the energetic trade-off in the inefficiency of locomotion inherent with smaller mass: during energetically stressful periods or seasons for surface activity, the energetic savings of torpor in the burrow might more readily promote positive energy balance. An alternative explanation for the evolution of torpor in smaller heteromyids as a trade-off for locomotor inefficiency might simply be the inability of individuals of small mass (and a high surface:volume ratio) to increase heat production sufficiently to offset heat loss during extreme cold, resulting in hypothermia. This alternative would be independent of food-finding ability. The evidence that torpor was developed in heteromyids at or prior to the locomotor dichotomy is that it occurs in both *Perognathus* and *Dipodomys* (see earlier); it is a finely tuned energy-conserving device in the former (Fig. 3), but is only latently present in the latter and is likely a relational capacity.

Both *Perognathus* and *Dipodomys* were present in upper Tertiary times (Lindsay 1972, Shotwell 1967, Reeder 1956, Wood 1935), long before the formation of true deserts in southwestern North America (Axelrod 1950). Voorhies (1974, 1975) has described as fossils a *Perognathus* sp. and a bipedal kangaroo rat (*Eodipodomys celtiservator*) preserved in their burrows in early Pliocene deposits in northeastern Nebraska. Preserved with them were seed hoards indicative of their granivorous habits, and their habitat was interpreted to be a riverine area traversing a grassland with a mild, equable climate. Shotwell (1967) describes fossil *Dipodomys* spp. and *Perognathus* spp. from the middle Pliocene of Oregon with no reference to probable habitat, and Lindsay (1972) reports the presence of *Perognathus* spp. in middle Miocene deposits in what is now the Mojave Desert of California, again with no reference to probable habitat. It is apparent that *Perognathus* and *Dipodomys* were geographically wide-spread throughout much of southwestern North America in upper Tertiary times, and inhabited areas predominantly grassland and semiarid in nature (Reeder 1956).

The formation of true deserts resulted from the late Pliocene-Pleistocene uplift of the Sierra Nevada-Cascade axis, together with the transverse and peninsular ranges of California and Baja California and the ensuing rainshadow effect (Axelrod 1950, 1958). *Perognathus* and *Dipodomys*, representing lineages that for many millions of years had been subjected to progressive aridity, likely were preadapted to a desert existence, and occupied this still more arid, new environment without much further modification.

Bipedalism, as exhibited by *Dipodomys* species, would by my scenario have developed in semiarid, open habitats, likely grasslands, as an aid in traversing the expanses between foraging sites. It represents an adaptation that could then readily be exploited in desert habitats. Although there is no evidence that bipedal locomotion in *Dipodomys* confers a direct energetic advantage (Fig. 4), I think there can be no question that it provides some as yet undefined relief (i.e., foraging advantage) from energetic constraints that would be imposed on a quad-

rupted of the same mass and habitat. The evidences for this statement are these: (1) in spite of relatively large mass and large absolute energy requirements while living in habitats of limited seed production, torpor is seldom if ever used; (2) a fixed, intermediate level of water regulatory efficiency restricts seed usage to those higher in carbohydrate composition and therefore higher in MWP (MacMillen and Hinds, 1983); and (3) cheek pouch volume (i.e., food-carrying capacity) in granivorous *Dipodomys* spp. is independent of body mass, but it is strongly and positively correlated with body mass in quadrupedal heteromyids (Morton et al. 1980). Thus, accompanying bipedality in *Dipodomys* are several characteristics that can be construed as energetically liberal, at least in comparison with their quadrupedal cousins, whom they typically exceed in biomass when sympatric (pers. obs.). Yet to be demonstrated are the direct advantages of bipedality in heteromyids; among these is the likelihood of enhancing predator avoidance and escape, but others should not be dismissed without trial.

Another mystery among heteromyids, at least to me, is *Microdipodops*, which inhabits exclusively Great Basin deserts. Their habitats are not only arid but of high elevation, and, therefore, have markedly truncated growing seasons. They are mysterious because virtually nothing is known of their origins, or whether they are more closely related to *Perognathus* or *Dipodomys*. Authorities align them more closely with one or the other (Hafner 1978, Lindsay 1972), not particularly close to either (Reeder 1956), or change their minds (Wood 1931, 1935). This lack of agreement is due largely to the absence of a fossil record. It is due in part, too, to the bipedal mode of locomotion in *Microdipodops* and the assumption that this implies close relatedness to *Dipodomys*. Nevertheless, Wood (1935) emphasizes that bipedalism has arisen several times independently in heteromyids, including extinct lineages only remotely related to extant genera; I see no reason to doubt an independent origin of bipedalism in *Microdipodops*. *Microdipodops* are also mysterious from a physiological point of view. To me they represent an enigmatic compromise that combines the water and energy regulatory virtues of *Perognathus*

and *Dipodomys*: they are small in size with low absolute energy requirements and efficient water regulatory capacities; they utilize torpor most propitiously; and they are bipedal. They are deserving of more attention.

The family Heteromyidae is a rather diverse group of rodents with respect to their adaptive physiology. Yet, when interpreted in light of locomotor and size differences within the family, together with paleoclimatological histories, discernible patterns emerge that are consistent both evolutionarily and ecologically.

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